

Catalogue of American Amphibians and Reptiles.

AUFFENBERG, WALTER AND RICHARD FRANZ. 1978. *Gopherus*.***Gopherus Rafinesque***
Gopher tortoises*Gopherus* Rafinesque, 1832:64. Type-species, *Testudo polyphemus* Daudin, 1802, by monotypy.*Xerobates* Agassiz, 1857:446. Type-species, not designated.*Bismachelys* Johnston, 1937:439. Type-species, *Bismachelys canyonensis* Johnston 1937, by monotypy.

- CONTENT. Four extant species are recognized: *G. agassizii*, *G. berlandieri*, *G. flavomarginatus*, and *G. polyphemus*.

- DEFINITION. A Nearctic genus of tortoise with flattened forelimbs and flat, broad claws adapted for digging. The cervical scute is usually as wide as long. The hypoplastron is usually longer than the hypoxiphiplastral, and the hypoxiphiplastral articulation is broadly emarginate. The cervical and caudal vertebrae are short and broad. The triturating surface of the premaxillaries possesses a distinct median ridge.

- DESCRIPTIONS. The skull, shell, and relationships are described by Williams (1950a, 1950b) and Auffenberg (1976), skull only by Gray (1873), carpus by Auffenberg (1966), os transiliens by Bramble (1974), mental glands by Winokur (1973), zoogeography by Blair (1958) and Brattstrom (1961), and general habits by Rust (1938).

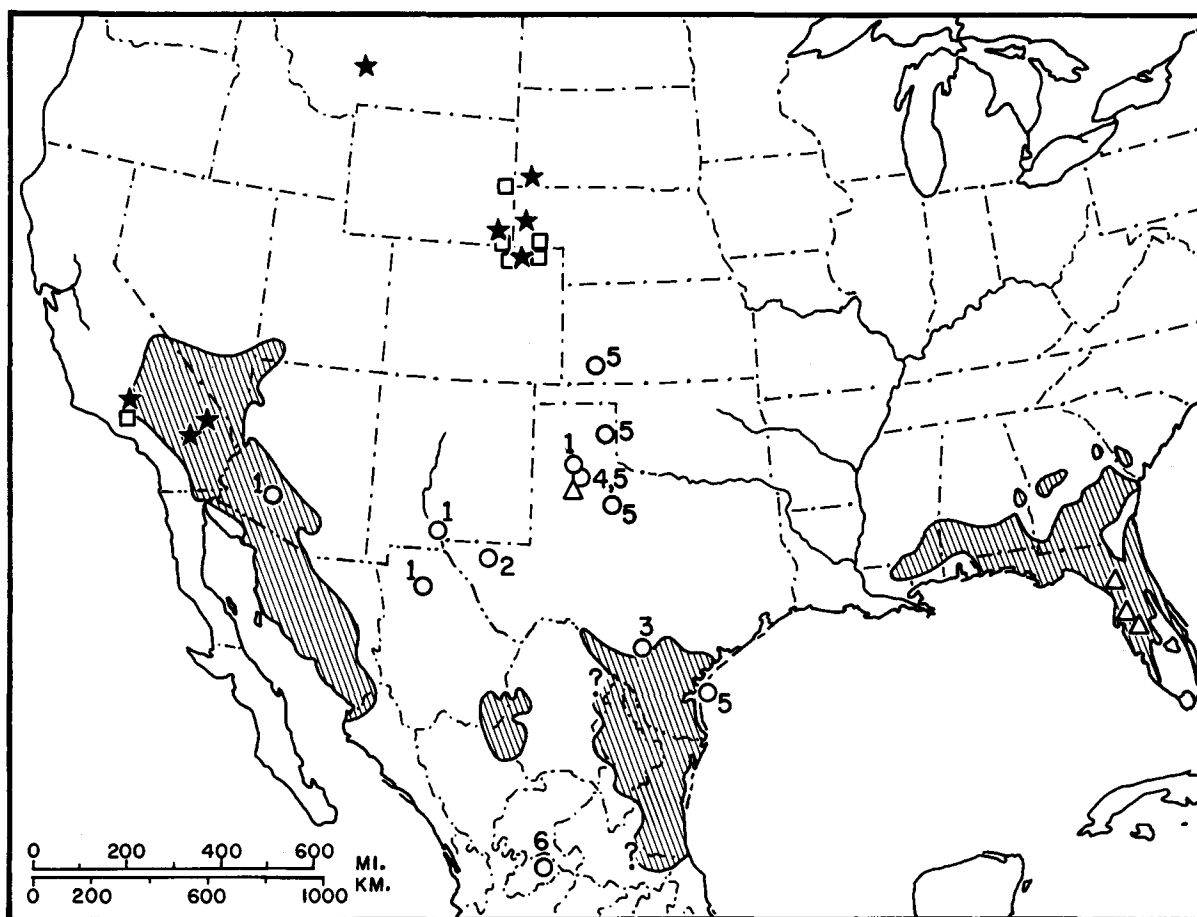
- ILLUSTRATIONS. See Auffenberg and Franz (1978a-d).

- DISTRIBUTION. The present range of *Gopherus* includes southeastern and extreme southwestern United States, southeastern Texas, and northeastern, northwestern and northcentral Mexico. Gopher tortoises are restricted to subtropical, subhumid to arid steppe, savannas, thorn brush, and desert biotopes.

- FOSSIL RECORD. Twenty-three species of *Gopherus* occur as fossils from the early Oligocene through the Pleistocene. Three of the four extant species—*agassizii*, *flavomarginatus*, and *polyphemus*—occur as fossils, primarily from Late Pleistocene deposits. Other Pleistocene species are *atascosae* (Middle), *auffenbergi* (Middle), *canyonensis* (Early), *hexagonatus* (Middle-Late), *huecoensis* (Early), and *laticaudatus* (Middle). *G. pertenuis* comes from the Late Pliocene, and an undescribed species (close to *polyphemus*?) is found in the Pliocene of Florida (in Florida State Museum collection). *Gopherus brattstromi*, *copei*, *dehiscus*, *mo-havetus*, and *pansus* are from the Late Miocene, and *G. brevis-ternus*, *edae*, *emiliae*, *hollandi*, *undabunus* from the Early Miocene. *G. laticuneus*, *neglectus*, and *praetians* are Early, Late, and Middle Oligocene species, respectively. For references to fossil species except *auffenbergi*, see Auffenberg (1974); for *auffenbergi*, see Mooser (1972).

- PERTINENT LITERATURE. For discussion of generic characters, see Williams (1950a); serology, Frair (1964); behavior, Eglis (1962); parasites, Petter and Douglass (1976). Douglass (1975, 1977) summarized the gopher tortoise literature in subject indexed bibliographies. For general accounts, see Carr (1952), Auffenberg (1969), and Ernst and Barbour (1972). Other important references are in Auffenberg and Franz (1978a-d).

- KEY TO THE LIVING SPECIES. Parenthetic numbers refer to published Catalogue accounts.



MAP. Recent distribution of *Gopherus* shaded. Records of Tertiary forms as follows: squares, Oligocene; stars, Miocene; triangles, Pliocene. Extinct Pleistocene species are: (1) *canyonensis*; (2) *huecoensis*; (3) *atascosae*; (4) *laticaudatus*; (5) *hexagonatus*; (6) *auffenbergi*. For fossil records of living forms, see Auffenberg and Franz (1978a, 1978c, 1978d).

1. Distance from base of first claw to base of third claw on forefoot equal to distance from base of first claw to base of fourth claw on hind foot 2
- Distance from base of first claw to base of fourth claw on forefoot equals to same measurement on hind foot 4
2. Carapace from above generally narrower posteriorly than anteriorly; usually one enlarged femoral spur; single axillary scale generally triangular or at least pointed posteriorly; cervical scute always single; no projections at outer ends of marginal sulci on either side of cervical scute; carapace ground color brown, laminae often with yellowish centers, plastron usually clear yellow *polyphemus* (215)
- Carapace from above generally narrower anteriorly than posteriorly; usually two enlarged femoral spurs; single rectangular axillary scale wider posteriorly than anteriorly; cervical scute frequently divided; usually obvious projections at outer ends of marginal sulci on either side of cervical scute; carapace ground color yellow, laminae with dark brown centers, plastron yellow with darker markings in some specimens *flavomarginatus* (214)
3. Snout wedge-shaped from above; axillary scales often paired; gular projections often divergent in large males; carapace ground color brown to black, laminae often with yellowish centers, head usually black with evident yellow temporal patches *berlandieri* (213)
- Snout rounded from above; axillary scales single; gular projections not usually divergent in adult males; carapace ground color brown, laminae often with yellowish centers, head usually brown, without lighter temporal patches *agassizii* (212)

• REMARKS. Wermuth and Mertens (1961) considered all extant *Gopherus* to belong to a single polytypic species, *G. polyphemus*. The geographic discontinuity of the four taxa, their behavioral and morphological differences, particular skull, shell, and foot structure, indicate that each is a distinct species (Auffenberg, 1976).

• ETYMOLOGY. The generic name, *Gopherus*, is derived from gopher, a partly phonetic spelling of the French word *gaufre*, meaning waffle. Gopher was a name applied by early French settlers in North America to any small burrowing animal. Also presumably from the same derivation is the name mungofa, applied specifically to the tortoise, derived from a West African word *gofa*, meaning to dig. The gender of the name *Gopherus* is masculine.

COMMENT

Auffenberg (1974) restricts the genus *Gopherus* to the Nearctic. Reference of the genus to the Tertiary of Asia by Williams (1952) was based on (1) a presumed relationship between *turgida* and *kalganensis* (most certainly correct), and (2) reference of *turgida* to the genus *Gopherus* (certainly incorrect, see Oelrich, 1957; Auffenberg, 1962). Auffenberg (1974) recognizes 19 extinct species of *Gopherus*, extending back to the lower Oligocene. A different interpretation of the fossil record and morphology of *Gopherus* is presented in Bramble's unpublished dissertation (1971). Fossil gopher tortoises are recorded from Montana, south into Mexico to at least Aguascalientes. The early evolution of the genus is correlated with the development and spread of xeric Madre-Tertiary floras in the intermontane basins of western North America.

By at least mid-Pleistocene, *Gopherus* was divided into the two species groups recognized today: the *polyphemus* group, *G. polyphemus* and *G. flavomarginatus*; and the *agassizii* group, *G. agassizii* and *G. berlandieri* (Auffenberg, 1966, 1976). However, Grant (1960) suggested that *Flavomarginatus* is more closely allied to *agassizii*, a view not followed here. The only sympatric occurrence of both the *polyphemus* (*flavomarginatus*) and *agassizii* (*auffenbergi*) groups is from the Pleistocene of Aguascalientes, Mexico.

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